The University of Chicago

THE ROLE OF THE SENSE ORGANS IN AGGREGATIONS OF AMEIURUS MELAS

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZÖOLOGY

By
EDITH STEELE BOWEN

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CHICAGO, ILLINOIS

Reprinted from
Ecological Monographs
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VOL. I JANUARY, 1931 No. 1

THE ROLE OF THE SENSE ORGANS IN AGGREGATIONS OF *AMEIURUS MELAS*

BY

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THE ROLE OF THE SENSE ORGANS IN AGGREGATIONS OF *AMEIURUS MELAS*[1]

Introduction

The young of the siluroid fishes, the catfishes and bullheads, exhibit a striking type of aggregation which by its apparent simplicity offers a tempting study to one interested in the fundamental bases of group behavior in animals. In the species *Ameiurus melas* (Rafinesque), used in this work, the young, when observed in the summer months in ditches and small ponds, are usually in a close cluster, swimming slowly near the surface, and packed together into a more or less spherical mass so that individuals are frequently in contact. A single fortunate dip with a net has been known to take five hundred, even when a large part of the group was seen to escape. Sometimes in shallow ponds on a warm sunny day large numbers may be seen resting at the surface in close proximity to one another. When disturbed they quickly dart down into the water, and scatter in all directions. In the latter part of the season the groups are often fairly small, sometimes consisting of a dozen individuals or less.

If a group in a small ditch is scattered its reformation may be observed. Several minutes after the disappearance of the fish two or three individuals appear singly and come together into a region somewhere near the original location of the group. Gradually they are joined by single individuals or small groups which come, apparently by random swimming, into the same locality. These smaller groups take no definite direction toward the larger one until they are within a short distance, about two or three feet. Then they swim directly toward the larger aggregation and join it. This larger group continues to attract others until it has reached its original size. This procedure took from half an hour to an hour in the cases observed. The fishes always appeared from the muddy bottom singly or at most in small groups.

When brought into the laboratory, the young aggregated for several days in the aquarium. Three hundred or more would collect in a cluster three or four inches in diameter, usually against the side of the aquarium. When undisturbed for some time they would frequently be more or less scattered, but with a slight disturbance would collect again. An unusual disturbance would always scatter the group as in nature. After some time in the laboratory the aggregations grew less frequent, but could always be produced by striking the aquarium. During the winter the aggregations lost their com-

[1] This problem was undertaken at the suggestion of Dr. W. C. Allee whose stimulating interest and helpful suggestions have been deeply appreciated. The present investigation was aided in part by a grant to the University of Chicago from the Rockefeller Foundation.

pactness; individuals were more frequently isolated, but usually aggregated when active. By strong stimulation, as in some of the experiments where the animals were placed beneath a bright light, aggregations could be induced at any time.

There has never been observed an indication of any specialization of function among the members of an aggregation. Leadership always falls to the fish which happens to be in the van. When the group turns, even slightly, leadership changes to the individual farthest in that direction. Two schools mixed readily when near together, and in the laboratory aggregations were formed when the largest fishes were three times the size of the smallest. The location of individuals in a school continually changes, but the form of the group itself remains much the same.

The breeding behavior of these fishes has been known since the time of Aristotle who observed it in the "Glanis." According to his description the eggs were laid among the roots of trees, and then the female, having spawned, departed, while the male watched and protected the young for forty or fifty days, until the young were sufficiently grown to escape from other fishes. Agassiz (1856), identified the "Glanis" as a siluroid closely related to our catfish and bullheads, and described similar behavior for Pomotis and Pimelodus in this country. Similar observations reported by others have been reviewed by Kendall (1910). The only reference to *Ameiurus melas* found so far in the literature is that by Fowler (1917), in which he gives a description, taken from notes by Dr. Van Dorn, of a pair spawning in an aquarium:

"Both sexes assumed charge of the nest and both guarded the young. Both parents remained in the nest at the same time, and at alternate times. The female was apparently the more savage and the male would bite one's finger when disturbed. The nest was a shallow depression, scooped out of the bottom, and its diameter about equal to the fish's length. The eggs, when deposited, were 200, and of a pale, creamy-yellow color. As the water was warm, they hatched in five days."

The sense organs of Ameiurus and their part in the behavior of individual fishes has been studied by several investigators. Herrick (1902), showed that in *Ameiurus melas* taste buds are present on the skin over the whole body, being especially abundant on the barblets, and that practically the whole cutaneous surface is sensitive to both tactile and gustatory stimuli. The olfactory organs were shown by Parker (1910), who worked with *Ameiurus nebulosus* (Le Sueur), to be distance receptors of chemical stimuli, and distinct from the chemical organs in the skin which are taste organs. He concludes that the senses of taste and smell differ in degree rather than in kind. According to Parker and Van Heusen (1917), Ameiurus is stimulated by metallic rods, probably through the gustatory organs. They also, (1917a), demonstrated that the ear, skin, and lateral line organs are all sensitive to vibrations. The

ear responds to wave lengths of greatest frequency, the lateral line organs to intermediate wave lengths, and the skin to the slowest vibrations. They found that the responses to the stimulation of the ear and of the skin are generally locomotor; those of the lateral line organs, inhibitory to movement.

While the eyes are probably of little importance in feeding, (Herrick, 1902; Parker, 1910; and Olmstead, 1918), Schiche (1921), from his study of the individual behavior of *Ameiurus nebulosus,* believes that the eyes are the controlling sense organs in the decidedly negative reaction to light, and in the orientation toward light. He states that optic sensitivity must be concerned in the control of movement since blind fish may remain in constant motion for a day at a time. A marked thigmotactic reaction is exhibited by these fishes, resulting in resting positions which bring as many points of the body as possible in contact with solid objects. This is illustrated by the "living-holes" or depressions which they make in the substratum, and to which they return at intervals. When the fish are subjected to conflicting stimuli, the chemical stimulus is the strongest, while thigmotactic and phototactic stimuli result in a response intermediate between those called forth by the separate stimuli.

In regard to the function of the sense organs in the aggregation of young fish, Eddy (1925), reported that blinded fishes do not aggregate. At that time he gave results, upon the effect of drugs and (1926) upon determinations of oxygen consumption which indicate that aggregating behavior is correlated with a relatively high metabolic rate.

Parr (1927), in a study of schools of typical pelagic fishes, reaches the conclusion that the behavior of individuals is controlled by visual stimulation alone. He believes, however, the catfishes (*Ameiurus*) are probably exceptional in this respect and that in their schools, which are globular and very dense, schooling and milling are dominatingly controlled by tactile stimulations.

The present work has been done in an attempt to analyze more fully the roles played by the different sense organs in the aggregations of catfishes.

Methods

The fishes used in this investigation were of the species *Ameiurus melas* (Rafinesque), and ranged in length from two to five centimeters. Two different types of experimental procedure have been employed. The first method was that of "preference" experiments carried out by means of gradient tanks. Here normal fishes were used in most cases, and the attempt was made to discover to what kinds of stimuli they gave a positive or negative reaction. In the second group of experiments the different sense organs were destroyed or rendered temporarily inactive, and the reactions of animals in a group were studied. The results of these two groups of experiments will be given separately and the evidence from the two methods discussed later.

Gradient Tank Experiments

Two different types of gradient tanks were employed in these experiments, but the principle was the same in both. A single fish placed in a long trough was allowed to swim back and forth, while the conditions introduced from the two ends could be made to vary in one particular only. The amount of time spent on the two sides of the trough was recorded by means of two stop watches. One measured the total duration of the experiment, 15 minutes in each case, while the other recorded the time spent on one side, *e.g.* the left. The time on the right side was then found by subtraction. The path of the fish was also recorded. In the great majority of the cases the fish was in motion most of the time, swimming back and forth or pushing against the ends of the tank. Since fishes varied in their individual tendencies to stay on one side or the other, a control for each experiment was run where the conditions were the same on both sides of the trough. Each series consisted of ten experiments. The percentages of the time spent in the same end of the experiment and the control were compared, and for both the experiment and the control

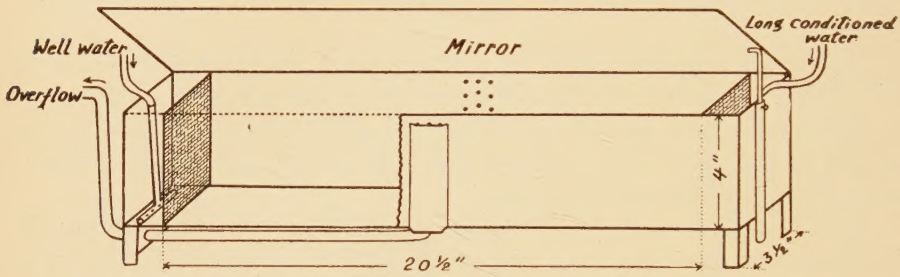

Fig. 1. Tank A, gradient tank for running water.

the percentage of time for one end was compared with the the fifty percent expected from random movements. The mean difference for each comparison is given with its statistical significance as calculated according to Student's Method. Values of .01 or below, indicating one chance or less in one hundred of as great variation from random sampling, are considered significant, those above .01 not significant.

Tank A (Figure 1) was arranged so that a slow current of water, three to four liters in fifteen minutes, entered at each end, and left through holes at the middle of the trough leading into an outlet pipe. The level of the opening of this pipe was adjustable and regulated the level of the water in the trough. The tank, make of galvanized iron, contained a wire screen at each end, and a wide meshed wire lining (not shown in the diagram) standing ½ in. from the sides of the tank to prevent the fish from coming into direct contact with the inlets and outlets. A mirror was arranged at an angle over the tank so that the image from the inside was reflected to the side and down, and the fish could be watched without the observer bending over the tank. The water

was siphoned from pans elevated about three feet above the tank, and entered the tank through two small brass pipes containing five openings and placed horizontally, one at each end. The tank was first filled with control water and then the current was started at both ends simultaneously, and at the same rate by the regulation of clamps. When colored water was employed a distinct line of division was observed in a few minutes at the middle of the tank with clear water at one end and colored water at the other. This tank was designed by Dr. Allee who suggested its use in this work.

The experiments were run in a dark room with two lights of the same intensity (40 or 50 watts) placed above and to the side of the tank, one on each side opposite the halfway point between the middle and the end of the trough. Thus the lighting was the same for both ends.

Tank B was simpler, consisting of a long trough of galvanized iron, 3 ft. long, 3½ in. wide, and 4 in. deep, with a mirror attached as in Tank A. The inside of this tank was covered with paraffin to prevent any action of metals, as Parker and Van Heusen (1917), have shown *Ameiurus nebulosus* to be stimulated by the dissociation of metals in water. This precaution was not feasible in Tank A because of the numerous small openings, but it is doubtful if this interfered to any extent with the results since the amount of metal on both sides was the same. The behavior of the fishes did not differ noticeably in the two tanks. In Tank B movable partitions could be placed at desired distances from the ends so as to give as long a gradient as possible and leave room at one end for a group of fishes. Only one 50 watt light placed opposite the middle of the tank was needed for lighting.

Well water used for these experiments was always allowed to stand overnight in large pans. This brought the oxygen content, as shown by Winkler's method, and the temperature to that of the aquaria. pH, which ran about 7.5—7.6 in the well water, was brought to the same point as that in the aquaria by adding a few drops of concentrated NaOH. The pH of the aquaria varied from 8.0—8.4 depending upon the length of time since well water had been added.

Series I and II. Tank A was used with clear conditioned water entering at one end, and well water colored with methylene blue entering at the other. The dye was added to permit observation of the currents. In the controls clear well water was run against colored well water. The conditioned water for this experiment had stood in the aquarium for several months, and had contained a variety of animals besides catfish. It was therefore water which had been highly conditioned heterotypically. The pH ran up to 8.4, which rarely occurred in other experiments. In five sets of each series the conditioned water was introduced from the left, in five from the right, to offset any tendency of the fishes to stay in one end. In the same way the order of the experiment and the control was varied with a rest of approximately 30 minutes between to offset any possible effect of a conditioned automatism

since catfishes tend to form place associations (Schiche, 1921). The fishes were from the same tank from which the conditioned water was taken.

When the percentage of time spent in the conditioned end of the experiment was compared with the percentage of time spent in the same end of the control, there was found to be a mean difference of 29.6% in favor of the conditioned water, with a significance of .0006. When, however, the time spent in one end of the control was compared with the 50% expected from random movements, there was found to be a mean difference of 28.2% in favor of the colored end with a significance of .000,000,1-. There is therefore a decidedly positive reaction to the colored water which agrees with the negative phototactic reaction of *Ameiurus* as described by Schiche (1921). In the experiment the factors of color and conditioning counteract each other and give no significance, but a definite tendency toward the conditioned water is shown by the comparison of the experiment and the control.

Series III and IV. These two series were the same as I and II except that no color was used. When the conditioned end was compared with the same end in the control there was found to be a mean difference of 22.15% in favor of the conditioned end with a significance of .0004. The experiments gave a mean difference of 11.65% in favor of the conditioned end with a significance of .005. These results indicate a positive reaction to highly conditioned water as against unconditioned well water by fish adapted to this amount of conditioning.

Series XI and XII. In these experiments well water conditioned for 45 minutes by 10 fish per 18 liters was run against unconditioned well water. In the controls unconditioned well water was run on both sides with the following results:

	Mean difference	*Significance*
Cond. end of experiment vs. same end of control....	.85—for cond.	.8541
Cond. end of experiment vs. 50%.....	3.05+for cond.	.3446

Although there is a slight tendency toward a positive response here the results are of no significance and probably indicate indifference.

Series XIII and XIV. These experiments were similar to Series XI and XII but the conditioned water was taken from a trough 11 ft. 6 in. long, 1 ft. 8 in. wide, and containing 6 in. of water, in which three large fishes and three turtles had lived for 10 to 12 days. This should test for any positive response to heterotypic conditioning. The results were:

	Mean difference	*Significance*
Cond. end of experiment vs. same end of control....	1.4 +for cond.	.8208
Cond. end of experiment vs. 50%.....	4.55+for cond.	.1934

The very slight tendency toward the conditioned water is insignificant.

Series XIX and XX. In all of the foregoing experiments it is possible that the conditioning of the water which favors survival in many aquatic

animals may have produced a tendency toward a positive response which had nothing to do with the aggregating behavior of the fish. Therefore in this set of experiments conditioned water of two types was used, one conditioned for one hour by 50 small catfish per 18 liters, and the other conditioned for the same length of time by an equal number of mud minnows, *Umbra limi* (Kirtland). For the controls unconditioned well water was run on both sides. These experiments were run July 23 to August 2, at a time when the catfish were aggregating closely. The animals used in these experiments had been in the laboratory for one to two weeks, and were aggregating most of the time and always when even slightly stimulated. Experimental summaries showed:

	Mean difference	*Significance*
Catfish cond. end vs. same end of control	1.1—for catfish	.8380
Catfish cond. end of experiment vs. 50%	2.7+for catfish	.5050

If there is any response to a specific conditioning it seems that it should have shown under the conditions of this experiment. The results, however, are decidedly indifferent.

Series XXI and XXII. In these experiments, run in Tank A, unconditioned well water was run against water from an aquarium 8 ft. long, 2 ft. wide, containing 10 in. of water in which about 50 catfish had lived for two months, August to October. The experimental animals were taken from another aquarium of approximately the same dimensions. They had been in the laboratory for about a month, and were still aggregating to a considerable extent. The results:

	Mean difference	*Significance*
Cond. end of experiment vs. same end of control	4.75—for cond.	.3446
Cond. end of experiment vs. 50%	2.7 —for cond.	.9214

The results here are definitely indifferent, showing no positive response to the catfish conditioned water.

Series IX and X. These experiments were run to determine whether there could be demonstrated a direct response to a conditioned gradient produced by a small group of catfish in quiet water. Tank B was used with wide meshed wire partitions (covered with paraffin) and placed 3 in. from one end and 9 in. from the other. The 9 in. end was on the left in Series IX and on the right in Series X. The experimental animals were two blind fishes whose eyes had been destroyed one week before, and which had since been kept in an aquarium by themselves. They had apparently fully recovered from the operation. Well water was placed in the tank and changed after each experiment and each control. Ten normal fishes were placed in the 9 in. end for the experiments as the conditioning factor. The order of the experiment and control was varied as in the preceding series.

When the time spent in the conditioned end of the experiment was compared with the time spent in the same end of the control, there was found to

be a mean difference of 22.3% in favor of the control with a significance of .0002. In the experiment there was a mean difference of 11.25 in favor of the end away from the group with a significance of .0008. This indicates a negative response to the group. That this was due to effects from the shock of the operation is doubtful when the normal behavior of the operated animals used in aggregation experiments is considered. A more probable explanation seems to be the previous isolation from the group. This is supported by the results of the next series. A sensitivity to conditioning, if present, was not sufficient under the conditions of this experiment to call forth any positive response.

Series XVII and XVIII. This set of experiments was exactly like IX and X except that the blind fishes were kept with the group, both before and between the experiments. Here the results were indifferent:

	Mean difference	*Significance*
Group end of experiment vs. same end of control	11.5—for group	.1666
Group end of experiment vs. 50%	3.4+for group	.5960

Isolation was apparently the cause of the negative results shown in Series IX and X.

Series XV and XVI. These series were similar to IX and X, but closely woven black cloth was placed over the wire meshed partitions and normal fishes from the group were used as experimental animals. The results were as follows:

	Mean difference	*Significance*
Group end of experiment vs. same end of control	9.05—for group	.2448
Group end of experiment vs. 50%	.35+for group	.9606

Here normal fishes showed no response to a group of fish out of sight, and so gave no evidence of a positive response to a conditioned gradient.

The controls of these series with Tank B show a tendency for the fishes to stay in the 9 in. end of the tank which is significant in one of the sets, Series IX and X. The reason for this was not determined. The opposite tendency in the experiments of Series IX and X with isolated blind fishes when a group was in the 9 in. end counteracts this sufficiently to give the results significance, and is probably therefore a true indication of a modification of behavior due to isolation.

A summary of the results of the experiments with gradient tanks is given in Table I. There is no evidence that a conditioning of the water, as by some chemical substance secreted by fishes into the water, plays any important part in the aggregation of catfishes. The only positive results were obtained with very highly conditioned water by fishes which had been living in that water, and this may very well have been due to an adaptation to a high percentage of waste products, or some such factor. Since the aggregations are formed very quickly, often in the course of a few seconds, it seems improbable that a response of this type is important. These results indicate that the olfactory

organs are not concerned in this group reaction, since according to Parker (1910) they are the organs through which a distance perception of a chemical substance must occur. This does not, however, exclude the possibility of a gustatory response associated with a contact stimulus.

The negative response to the group obtained from the blinded fishes which had been isolated needs further investigation. It may be that isolation has some effect upon the reaction to vibrations which seems to be the stimulus, if any, which was effective.

TABLE I

GRADIENT TANK EXPERIMENTS

FLOWING WATER IN TANK A

Series	*Conditions*	*Mean difference in %*	*Significance*
I, II	Colored well water vs. long conditioned water	1.4	.8514
		.....29.6	.0006
	Colored well water vs. clear well water	28.2	.000,000,1—
III, IV	Clear well water vs. long conditioned water	11.65	.005
		.....22.15	.0004
	Clear well water vs. clear well water	10.5	.0494
XI, XII	Well water vs. water conditioned for 45' by 10 fish per 18 liters	3.05	.3446
		..... .85	.8514
	Well water vs. well water	3.9	.3848
XIII, XIV	Well water vs. water conditioned heterotypically for 10 days	4.55	.1934
		..... 1.4	.8208
	Well water vs. well water	3.15	.4688
XIX, XX	Minnow cond. water vs. catfish cond. water	2.7	.5050
		..... 1.1	.8380
	Well water vs. well water	3.8	.3398
XXI, XXII	Well water vs. water cond. by catfish for two months	4.75	.3446
		7	.9214
	Well water vs. well water	4.05	.3956

QUIET WATER IN TANK B

Series	*Animals*	*Conditions*	*Mean difference in %*	*Significance*
IX, X	Isolated blind fish (wide meshed partitions)	← 0 fish vs. 10 fishes	11.25	.0008
			.....22.3	.0002
		→ 0 fish vs. 0 fish	11.05	.0084
XVII, XVIII	Blinded fish from group (wide meshed partitions)	- - - → 0 fish vs. 10 fishes	3.4	.5960
			.....11.5	.1666
		- - - → 0 fish vs. 0 fish	14.9	.0228
XV, XVI	Normal fish (black cloth partitions)	- - - → 0 fish vs. 10 fishes	.35	.9606
			..... 9.05	.2448
		- - - → 0 fish vs. 0 fish	9.4	.0967

* The arrows designate the end favored to the extent of the mean difference indicated. Where this is significant the arrows are represented by solid lines, where it is not significant by dotted lines.

TABLE II

Stages of aggregations of ten blinded fishes after given intervals of time.

	Exp. 1 — in light		*Exp. 2 — in light*		*Exp. 3 — in dark*	
	Interval	*Stage*	*Interval*	*Stage*	*Interval*	*Stage*
1	2′50″	5	1′	2	1′46″	5
2	2′30″	3	1′	4	1′21″	4
3	2′20″	4	1′	4	1′25″	3
4	2′10″	4	1′30″	3	1′15″	5
5	1′30″	3	1′	4	1′11″	4
6	1′05″	4	1′	4	0′58″	3
7	1′35″	4	1′	4	1′35″	3
8	1′03″	5	1′	4	1′14″	3
9	1′30″	4	1′	4	1′16″	5
10	1′02″	4	1′	5	1′50″	3

AGGREGATION EXPERIMENTS

In this part of the investigation groups of fish were used and their aggregating behavior was studied directly. The group was placed in a white porcelain tub, 3 ft. 3 in. by 2 ft. 1 in., which contained 3 to 4 in. of water. The experiments were carried on in a dark room. A 40 watt light placed over the center of the tub gave a fairly even lighting, and could be switched on and off at will. For convenience the following five stages in the degree of aggregation were decided upon, and the results recorded in terms of these stages:

Stage 1. Close aggregation, fishes in one or two compact groups.
Stage 2. Loose aggregation.
Stage 3. Slight grouping, one half of individuals near another fish.
Stage 4. Mostly scattered, less than one half of individuals near another fish.
Stage 5. Completely scattered.

In a tub of this size with ten fishes, there is a distinct difference between the extremes of this series. Stages 3 or 4 might possibly appear by chance in a few cases when actually there was no aggregation, but never Stages 1 or 2.

The operations on the different sense organs were in most cases performed according to the technique worked out by Parker (1917). The olfactory nerves were cut by an incision just posterior to the olfactory pits. The auditory nerves were cut by an incision between the ear and the brain. The lateral line organs in the head were destroyed with an electric needle, while the lateral nerves were cut by an incision at the anterior end of the lateral line canal. The skin was anaesthetized by treatment with a 10% solution of magnesium sulphate in most cases for two minutes. This was a more dilute solution and was used a shorter period of time than that employed by Parker, but the fishes used were small and a stronger solution or a longer treatment was either fatal or prevented all activity for an hour or more. In the experiments on older fishes treatment for five minutes was necessary to render them insensitive to touch. In blinding, the eyeball was destroyed with a hot needle in the first few cases. Sometimes this operation was not complete and a part of the eye was apparently reconstituted after a few days. Therefore in most of the animals used in this type of work the eyeball was removed completely. The fishes recovered rapidly with no fatalities. Blinders, as used by Parker, were not feasible on these small fishes. The reactions of the blinded fishes were in all cases such as was expected from the behavior of the normal fishes in the dark. They were active almost continuously and remained isolated from one another. For all of the operations the fish were anaesthetized in a solution of 10% ether in water until they were entirely inactive. This took from two to five minutes depending upon the size and condition of the fish.

Vision

The first three experiments were performed to test the statement made by Eddy (1925), that blinded catfishes do not aggregate. In Exp. 1 ten fishes which had been blinded by a hot needle two days before were placed in the tub and the stage of aggregation noted at given intervals. These trials were made in the light. In Exp. 2 and 3 ten fishes were used which had been blinded by the removal of the entire eyeball two days before. Exp. 2 was carried on in the light and Exp. 3 in the dark. In the last case the stage of aggregation was observed at the instant the tub was illuminated.

The results are shown in Table II. In no case was Stage 1 observed and Stage 2 in only one case, and that at the beginning of Exp. 2 before there had been sufficient time for the fish to separate to any extent. There is no indication of any greater aggregating behavior in the light than in the dark. This is in marked contrast to the aggregations of normal fish as will be shown later.

It seemed desirable to check these results by determining whether under any conditions normal fishes would aggregate in the dark. Preliminary observations were made on 100 small catfishes which had been brought into the laboratory about a week before. These were placed in the tub with a 40 watt Mazda light over the center. The behavior was noted as follows:

Light—Closely aggregated.
Dark for 1′ 43″—Loosely scattered.
Light—Aggregated closely in 2″.
Dark, followed by dim light from far end of room—Loose aggregation, very active.
Scattered mechanically—Equally distributed throughout the aquarium, active.
Light—"Streamed" together, 5 groups, then 2, then 1 in 30″.
Dim light for 3′—Even scattering over the aquarium.
Light—Aggregated in 3″.

A series of experiments was then run on groups of ten fishes to test more fully the relation of the stage of aggregation to the presence of light.

In Exp. 4 ten normal fishes were placed in the tub in the light, and the stage of aggregation recorded at ten second intervals for 20 trials. In all the observations the fishes were in a close aggregation, in Stage 1.

In Exp. 5 ten normal fishes were placed in the tub, left for intervals in the dark, and observed as the light was flashed on. The results in Table III show no close aggregation, and only one case of Stage 2 at the beginning. Observations after shorter periods in the dark showed that the amount of scattering varied directly with the time since illumination. In general the groups were in Stage 2 after 15″, in Stage 3 after 30″, and in Stage 3 or 4 after 45″.

When catfishes are scattered in an aquarium in the laboratory, as frequently occurs when the room has been quiet for some time, they will always aggregate quickly if the aquarium is struck once or twice. To determine whether the fishes would aggregate in the dark if disturbed, in Exp. 6 a series of ten trials was made with two parts to each. In the first part the stage of aggregation was observed after a period in the dark as in Exp. 5. In the second part a blow was struck on the tub three to five seconds before the light was turned on and the stage recorded. The results given in Table 3 show no aggregation of any significance in either part.

There was the possibility in Exp. 6 that there had not been time for aggregation in the dark which, if possible, might take longer than in the light. To check this in Exp. 7 twenty trials were run with observations made after several blows extending over a longer time than in the preceding experiment. The trials were run at four different times, five trials at each. There is no evidence of aggregation from these experiments.

TABLE III

Stages of aggregation of ten normal fishes in the dark with and without disturbances from blows.

	Exp. 5		*Exp. 6(a) No blow*		*(b) 3"-5" after blow*	
	Interval	*Stage*	*Interval*	*Stage*	*Interval*	*Stage*
1	0'54"	2	1'20"	5	1'10"	5
2	1'44"	5	1'30"	5	1'16"	5
3	1'40"	5	1'10"	5	1'30"	5
4	2'08"	4	1'27"	5	1'12"	5
5	1'52"	5	1'03"	3	2'05"	5
6	2'14"	5	1'07"	5	2'15"	5
7	1'03"	5	1'10"	5	1'07"	3
8	0'54"	3	1'15"	5	0'35"	3
9	1'40"	3	5'05"	3	0'40"	5
10	0'59"	3	0'55"	5	0'50"	5

	Exp. 7						
	(a) No blow		*(b) 3"-5" after blow*		*(c) Longer interval with blows*		
	Interval	*Stage*	*Interval*	*Stage*	*Interval*	*Blows*	*Stage*
1	1'39"	5	1'38"	5	1'45"	0'40"	3
2	1'29"	4	1'40"	5	2'12"	37"	5
3	1'52"	5	2'10"	4	0'52"	23"	5
4	1'15"	5	0'58"	5	1'13"	31"	5
5	1'54"	5	2'30"	5	1'34"	17"	5
6	1'10"	4	1'55"	5	1'51"	23"	5
7	1'57"	5	1'48"	5	2'14"	26"	4
8	1'58"	5	0'51"	3	1'30"	17"	5
9	1'13"	5	0'59"	5	1'07"	17"	5
10	1'06"	5	1'13"	5	1'22"	25"	5
11			1'27"	5	1'22"	20"	5
12			1'10"	3	1'40"	21"	5
13			2'05"	5	1'14"	33"	5
14			1'25"	5	1'33"	15"	5
15			1'26"	5	1'19"	15"	5
16			1'50"	4	1'35"	29"	5
17			1'40"	5	1'20"	20"	5
18			1'20"	5	1'53"	30"	5
19			1'15"	4	2'25"	24"	5
20			1'16"	5	2'08"	29"	5

Observations were also made at hourly intervals throughout the night on the behavior of catfishes in two aquaria in the laboratory. Aquarium A, measuring 8 ft. long, 2 ft. wide, and containing 10 in. of water, faced the window and had the sides of the left end covered with black paper. Aquarium B, measuring 4 ft. long, 2 ft. wide, and containing 10 in. of water, was located with the left opaque end toward the window and so in the shadow. The results from these observations are given in Table IV. They show no aggregation during the darker part of the night, a gradual increase in the closeness of aggregation as it began to grow lighter, with aggregations similar to those during the day at dawn. There was some illumination entering the window of the laboratory, so that the fishes were not in absolute darkness. Since, however, these fishes were collected from a ditch along a main highway frequently well lighted by passing automobile lights, the illumination was probably not much greater than occurred in their natural habitat. No

case of an aggregation approaching those typical of the daytime was observed in either aquarium during the night.

A group of catfishes give reactions to large moving objects which correspond closely to those reported by Garrey (1905) for a school of sticklebacks. They move in the opposite direction from the object and thus escape pursuit. To a small moving object about their own size they give quite a different reaction, and swim along parallel to it or directly behind it. This reaction is induced when a black paraffin model of a catfish is drawn through the water, or even when a piece of rubber of the same size is substituted.

All of the results on vision indicate that it is a limiting factor in the formation of aggregations, and that without it aggregations break up in the course of a few minutes. According to these results the catfishes must be scattered in very muddy water and at night, and come together where vision is possible. The reformation of a catfish aggregation after scattering in the ponds where they are found suggests that this is probably the case (p. 1).

Equilibration and Hearing

An attempt was made to determine whether the ear played any part in the aggregating behavior. The eighth nerves were cut by dorsal incisions on 12 fishes of which 10 survived for two days or more. The completeness of the operation was shown by the loss of equilibrium in all cases. This, however, interfered with any possible tendency to aggregate since the fishes could not direct their movements. They turned in spirals while swimming, and rested unless disturbed. No other attempt was made to ascertain whether hearing is concerned, but it seems extremely doubtful that it is. The only sound the young catfish were ever heard to make was a slight cracking noise when they opened their jaws widely. This occurred only when they were handled as in the anaesthetizing experiments, and was never observed in the aquarium.

Olfactory Sense

Two groups of fishes were used in these experiments. Group A consisted of eight fishes which survived from a group of ten which were operated upon July 16. Autopsies performed July 19 at the conclusion of the experiment showed seven of the eight operations to be complete. In three cases the olfactory nerves had been cut, in four cases the olfactory lobes were severed and in one instance the cerebral hemispheres were injured. Group B consisted of ten fishes operated upon October 10, all of which survived. On November 18 the operations were repeated upon five of these to offset a possible regeneration of the nerves, and at the same time the eyeballs were removed. Autopsies performed December 3 upon the four individuals still surviving showed that in these cases the operations had been complete.

In Table V are given the stages of aggregation shown by these two groups of fishes at intervals. It will be seen that the aggregating behavior was not at all affected by this operation.

A single experiment with normal fishes was performed in connection with the distance perception of chemicals from other fishes. Eight individuals were placed in a small aquarium, 10′ by 8′ by 8′, in which were suspended two cheese cloth bags, one containing a piece of glass rod, and the other two pithed catfishes. In 25′ there was no response to either bag, but with liver in place of the pithed fishes there were 58 nibbles at the bait in 30′ and four at the glass rod. In this last experiment the bags were interchanged at the end of 15′.

Another experiment was run with three live fishes tied in the cheese cloth bag. This was of 30′ duration with the bags interchanged at the end of 15′. Here there were five nibbles at the control and two at the bag which contained the fishes. This gave no indication of a perception of other fishes through the olfactory organs.

The results of these experiments agree with those from the gradient tanks in giving no evidence for any distance perception of a chemical as a factor in the aggregation of catfishes.

In some of the earlier experiments on blinded fishes it was observed that occasionally, in cases where there could be no question of the completeness of the operation, a blinded fish would turn toward another fish swimming past and sometimes follow it for one or two turns. This suggested that, whereas a fish can never keep close to another fish except by means of vision, it may be sensitive to the presence of another fish through other sense organs than the eyes. To determine whether this is so a series of experiments was run on blinded fishes, with and without other sense organs. A group of fishes, usually five, was placed in the porcelain tub. The blinded fishes remained scattered, ordinarily swimming at random around the tank. Each time two fishes passed within two inches of one another going in the opposite direction the reactions of both were noted. If one of the fishes turned toward the other or altered its direction as if to turn back and follow the other, it was considered a positive reaction. If neither gave any reaction, it was considered indifferent. If one fish turned away from the other without turning back it was considered a negative reaction. In any case where the stimulus may have been something besides the other fish (*e. g.* the side of the tub) the reaction was not recorded. These criteria were based on the similar but better directed reactions of normal fishes to each other. Since no positive reactions of blinded fishes were observed when the fishes passed at more than two inches from one another, this was taken as the maximum distance to be considered. In some of the experiments the reactions were also recorded when two fishes actually touched each other in passing. In some instances these showed a larger percentage of positive reactions, but there were usually fewer of them, and in many instances there were approximately the same proportion of types of responses as when there was no actual contact between the fishes. The experiments ran for 15′ in all cases.

The results are given in Table VI. Exps. 1 and 3 give the percentages with normal animals. In Exp. 2, the first one with blinded fishes, there was no indication of a positive response. The normal fishes, however, were not at this time showing typical aggregating behavior. Only two of the five blinded animals were active for most of the time, and almost all the positive reactions were given by these. The other three were resting, something which never occurs normally under the conditions of the experiment. This experiment was performed during very hot weather when the fishes were dying in large numbers. There were only 7 per cent positive reactions and these may well have been due to chance. In all the other experiments (4, 5, 6, 9, and 14) blinded fishes gave about 50 per cent of positive reactions. The results of Exp. 2 are included only to indicate that fishes in a poor condition do not give reactions. None of the other treatments given to catfishes inhibited locomotion, with the possible exception of treatment with magnesium sulphate.

By comparing the results of Exps. 7 and 8, in which the olfactory nerves were cut, with those in which the olfactory nerves were intact, it will be seen that the cutting of these nerves has no effect upon this response of the blinded fishes. After cutting the olfactory nerves there was 47.5 per cent of positive responses as compared with 47.8 per cent in fish which were blinded only. Positive responses similar to those produced by another fish were frequently observed if a paraffin model with a loose movable tail was drawn past a fish. In this case there was little or no possibility of a specific chemical stimulus.

TABLE IV

Observations at hourly intervals during the night upon two aquaria of young catfishes.

Time	*Large aquarium A*	*Small aquarium B*
11:00 P.M. (After several hours in light)	Loose aggregation behind dark paper	Active, more or less scattered
11:30 (After 30′ in dark)	Actively swimming and scattered, more in lighter end of aquarium	Same as A
12:00	Active, scattered, few more in lighter end	
12:05	(After 5′ in light with frequent blows) 2 small close aggregations in lighter part, large loose aggregation in darker part	(After 5′ in light) One large fairly loose aggregation in the light end
1:00	Active, scattered, many more near surface at lighter end	Same as A (After 1′ with jarring) One loose aggregation
1:05	(After 5′ in light) Two very loose aggregations, many scattered	
2:00	Scattered, but more in lighter end	Same as A

3:00	Same	Same
4:00	Evenly distributed in light third of aquarium	Loosely collected at light end
4:30	Same	Same
5:00	Loose aggregation, few scattered	Same as A
5:15 (Sunrise)	Aggregated	Aggregated

Perception of Vibrations

Since a chemical factor is apparently not concerned in the positive reactions of blinded fishes to one another, it seems possible that they may be due to the vibrations set up in the water by the tails of the fishes as they swim past one another. This is suggested by the fact that there seem to be more positive reactions when the fishes swim rapidly and vigorously than when they swim in a more leisurely manner. The tails vibrate about four to six times per second in fast swimming, and fairly regularly. As shown by Parker (1917) vibrations in water are received by Ameiurus through three sets of sense organs, the ears, the lateral line organs, and the skin. The most rapid vibrations, received by the ear, are probably not concerned with aggregation responses. Experiments were performed to determine whether the lateral line organs or the skin were concerned.

When the skin was anaesthetized with magnesium sulphate the percentage of positive reactions was very small, as shown in Exps. 10, 11, 12, and 19 (Table VI). This treatment tended to make the fishes more sluggish, but in both 11 and 12 the number of possible reactions was fairly large. As a partial control an experiment was performed in which fishes were given the same treatment with water. These fishes showed a much higher percentage of positive reactions, 35%, as shown by Exp. 13. Close aggregations were formed when fishes with normal vision were treated with magnesium sulphate (Table V), although these fishes were less active than untreated fishes and rested in groups a part of the time.

Fishes with lateral line organs destroyed aggregated in a normal way as shown in Table V. When blinded and tested for individual reactions, they gave a percentage of positive responses comparable to those given by blinded fishes with lateral line organs intact (Exps. 15 and 17). Apparently positive reactions were not dependent upon the lateral line organs. When these same fishes were anaesthetized with magnesium sulphate, the percentage of positive reactions was insignificant (7 and 8 per cent). These results indicate that the skin is the receptor of the stimulus responsible for aggregations. The average percentage of positive reactions for the experiments of each type and the number of possible responses for each are given in Table VII. Blinded fishes gave approximately 50 per cent of positive reactions, except when the skin was anaesthetized. Whether the reaction

to vibrations received through the skin is of any fundamental importance in this connection is questionable. It may be only a conditional automatism which has been developed in connection with the aggregating behavior. This point needs further investigation.

Tactile Reactions

Catfish, as shown by Schiche (1921), are strongly thigmotactic, always resting with as many points of the body as possible in contact with the substratum. This response also plays a very important part in the aggregating behavior of these animals, reinforced as it seems to be by a response to gustatory stimulation. When two fishes come to rest in an aquarium they are usually touching or very nearly so. When normal fishes are placed in a tub of water with black paraffin models, they will frequently approach a model, rub the barblets over it, and then turn away. This occurs repeatedly, whereas if they approach a resting catfish in the same way, they push against it several times and usually come to rest touching it or nearby. Such behavior was observed toward a sick fish resting on its side, and to a freshly killed fish held in place by a twig. In the latter case the living fish twice pushed against the dead one until it was dislodged and floated to the top. When mud minnows were placed with catfishes the latter approached a resting minnow, drew the barblets over it, pushed against it several times, and frequently came to rest in contact with the minnow if the latter remained quiet. Usually the minnow swam off. Catfishes follow mud minnows and goldfishes in the aquarium, but the minnows avoid the catfishes with a darting movement, and thus escape, while the goldfishes swim more rapidly, or dodge out of the way. When the barblets were removed the catfish still aggregated quite normally. There are indications here of a tactile-gustatory discrimination of some kind, but not such as enables a catfish to distinguish members of its own species.

TABLE V

Stages of aggregation of fishes with eyes intact and other sense organs inactivated.

	Olfactory nerves cut A. 8 fishes B. 10 fishes		*Lat. line organs destroyed* 5 fishes		*Skin anaesthetized* 8 fishes			
	Int.	*Stage*	*Int.*	*Stage*	*Int.*	*Stage*	*Int.*	*Stage*
1	1′30″	1	1′	1	1′	2	1′	2
2	1′	1	1′	1	1′35″	1	1′	1
3	1′	1	1′	1	2′	1	1′	1
4	1′07″	1	1′	1	1′30″	1	1′	1
5	1′20″	1	1′	1	1′30″	1	1′	1
6	1′03″	1	1′	1	1′	1	1′	1
7	1′	1	1′	1	0′30″	1	1′	1
8	1′20″	1	1′	1	1′	1	1′	1
9	1′	2	1′	1	1′	1	1′	1
10	1′	1	1′	1	1′	1	1′	1

TABLE VI

Individual reactions of fishes to others of group.

Condition	*No. of fishes*	*Non-touch reactions* +	—	0	*Tot.*	*%+*	*Touch reactions* +	—	0
1. Normal.....	5	147	2	13	162	91%	3	1	1
2. Blinded (2)*.....	5	5	8	58	71	7%	2	7	2
3. Normal.....	5	All aggregated whole period							
4. Blinded (2).....	5 (2 cm.)	14	1	20	35	40%	7	2	3
5. Blinded.....	5 (3.5 cm.)	28	1	25	54	52%	9	6	4
6. Blinded (11).....	5	26	0	21	47	55%	6	1	4
7. Blinded (11)..... Olf.N. cut (3)	5	25	1	21	47	53%	12	2	0
8. Blinded (2)..... Olf.N. cut (2)	5	5	0	7	12	42%			
9. Blinded (3).....	5	13	3	12	28	46%	5	0	3
10. Blinded (3)..... Tr. MgSO4	5	0	0	3	3	0%	0	0	0
11. Blinded (12)..... Tr. MgSO4	5	7 (4)	4	31	42	17%	5	7	5
12. Blinded (29)..... Tr. MgSO4	3	2	3	18	23	9%	3	2	2
13. Blinded (29)..... Tr. H_2O	3	7	2	11	20	35%	3	1	2
14. Blinded (31).....	5	25	0	29	54	46%			
15. Blinded (1)..... Lat. L. O. dest. (1)	5	27	0	28	55	49%			
16. Blinded (1)..... L.L.O. dest. (1) Tr. MgSO4	5	4	1	56	61	7%			
17. Blinded (57)..... L.L.O. dest. (2)	5	26	0	27	53	49%			
18. Blinded (60)..... L.L.O. dest. (5) Tr. MgSO4	5	2?	0	22	24	8%			
19. Blinded (61)..... Tr. MgSO4-5′	5	1?	0	12	13	8%			

TABLE VII

Percentage of positive reactions shown by passing fish
Summary of experiments

Normal *% Pos. Tot.*	*Blinded* *% Pos. Tot.*	*Olf. N. cut* *% Pos. Tot.*	*Lat.L.dest.* *% Pos. Tot.*	*Tr. MgSO4* *% Pos. Tot.*	*Lat.L.dest. &c tr. MgSO4* *% Pos. Tot.*
91% 162	(7% 71)	53% 47	49% 55	0% 3	7% 61
100%	40% 35	42% 12	49% 53	17% 42	8% 24
	52% 54			9% 23	
	55% 47			8% 13	
	46% 28				
	46% 54				
Aver. %					
95.5%	47.8%	47.5%	49%	8.5%	7.5%
Totals	176	59	108	81	85

*Numbers in parentheses indicate days which elapsed between operation and experiment.

DISCUSSION

Aggregations are of widespread occurrence throughout the different phyla of the animal kingdom, and are found in varying degrees of complexity; from the chance assemblages of animals resulting from some external environmental factor or group of factors, to the highly organized groups among social insects and man, based almost entirely upon the reactions of the individuals to one another, and containing undoubtedly what is usually known as a social element. When, however, an attempt is made to classify animal groupings and to draw a line of distinction between chance aggregations and those which are clearly social, many difficulties are encountered. Attempts have been made by several authors, but none of these are entirely satisfactory. They serve largely to emphasize the fact that there is no clear distinction between different levels of complexity in animal aggregations, but that a continuous series may be traced from the simplest to the most complex. This fact suggests the possibility that all animal aggregations may have some elements in common, and that analysis of some of the simpler cases may throw light on the more highly organized types of integration. The study of animal groups is included in what has usually been called general sociology.

To understand social behavior in animals, their integrations, and the nature of the satisfaction of the social drive or "social appetite" some sort of analysis is necessary. One logical approach to this problem is through a study of the sense organs. They must serve as the gateways by which all sensations from the external world reach the central nervous system, and therefore all stimuli from other individuals must pass through them. Analyses to determine the sense organs concerned in integrations and in the satisfaction of the social appetites should furnish a firmer basis for the classification of animal societies and knowledge of their evolution than a purely descriptive foundation. Aggregations of young catfishes are peculiarly interesting for studies of this kind. They belong among those groups of animals which have a distinctly social aspect as contrasted with chance aggregations of animals due to the force of external factors; and the degree of integration is high, as any one will appreciate who has seen one of the closely packed groups. But the organization is extremely simple, with nothing approaching in the slightest degree a morphological division of labor, and with the individuals of the mass constantly shifting in what is apparently a purely haphazard manner. Thus it seems possible here, if anywhere, to find clues to the fundamental reactions concerned in this type of social behavior. In addition catfishes are excellent experimental material. They survive operations very well, and considerable work has been done on their individual reactions.

The first sense organs which were studied by the writer in connection with the group behavior in young catfishes were the olfactory organs, a pair of pits located in the anterior end of the snout, and connected with the olfac-

tory lobes of the brain by the olfactory nerves. These were readily severed in the operated animals by a dorsal incision. Parker (1910) has shown that these organs function as distance receptors for chemical stimuli. The chemical receptors in the skin, the taste buds, are, on the other hand, sensitive to chemical stimuli when in more or less direct contact with them (Herrick, 1902; and Parker, 1910). Conditioning of the water by animals of the same or of other species has been found to have survival value for many animals (Drzewina and Bohn, 1928; Allee, 1929a, and citations). Various theories have been advanced to account for this fact, among them that of the secretion of some auto-protective substance into the water. It seemed possible that, if such group protection held true for young catfishes, individuals might collect into groups on account of the perception of some substance. At least it was possible that some specific chemical might serve as an integrating factor in the formation of the aggregations, even if no protective value were inherent in it. To test this possibility the gradient tank experiments were performed with water conditioned homotypically and heterotypically for varying lengths of time. Since catfish aggregations may form in a few minutes no long conditioning could be expected to effect them. In only one case did the results of the writer's experiments give support to the idea that aggregations were due to chemical substances. This was when highly heterotypically conditioned water was used. In this there must have been an overabundance of waste products, and the experimental animals used had been living in this water and had become adapted to it. This amount of conditioning could not effect ordinary aggregations.

It was yet possible that the aggregations might depend upon a specific chemical which would lose its effectiveness in the water and stimulate for only a short time after being given off. The experiments with the fish in the cheese cloth bags were performed to test this. The normal animals gave the expected number of positive reactions to liver suspended in the bags, such reactions as were shown by Parker (1910) to be due to a stimulation of the olfactory organs, but gave no more positive responses to bags containing pithed fishes than to those with a glass rod. It should be noted here that normal fishes showed positive reactions toward a pithed fish when actual contact occurred, and were able to distinguish it from a paraffin model.

The third piece of evidence in regard to the olfactory organs is from the experiments with operated animals. Fishes with eyesight intact, but with the olfactory nerves cut, aggregated in a manner in no way distinguishable from that of normal fishes. When blinded these fishes gave a percentage (47.5) of positive reactions entirely comparable to that (47.8) shown by blinded fishes with the olfactory nerves intact. The cutting of the olfactory nerves had no discernible effect upon the aggregating reactions.

From these three lines of evidence there is no indication that the olfactory sense organs play any part in social behavior of the young catfishes, or

that a specific chemical that can be perceived at a distance acts as an integrating factor, as is the case in some of the social insects. This is true in spite of the fact that the olfactory organs themselves are fairly sensitive and of primary importance in the feeding of catfishes (Parker, 1910).

Hearing has not been investigated with any thoroughness. Catfishes do have a fairly well developed sense of hearing as has been shown by von Frisch (1923), who has trained a catfish (*Ameiurus nebulosus*) to feed at the sound of a whistle. But since there is no evidence that catfishes make any sound while aggregating, it is unlikely that hearing is important in integration.

Sense organs which are of great importance in the integration of catfish aggregations are the eyes. This was shown by Eddy (1925). The results of this investigation have strongly corroborated his findings. Blinded fishes never aggregated, and in addition it was shown that catfishes do not aggregate in the dark, and that aggregations are broken up in about a minute after light is removed. Aggregations do not form in the dark even when the fishes are disturbed by noises and jarring, stimuli which almost always produce rapid aggregations in the light. All observations indicated that the fishes studied were in motion most of the time in the dark as are the aggregating fish in a lighted aquarium, but there was no schooling. Older fishes in the light usually rest in as shaded a region as possible, and when disturbed dart rapidly about as if highly stimulated. With small fishes the aggregating responses overcome the negative reaction to light when more than one fish is present. It can be concluded from these observations that the eyes are extremely important for integration and that without them the aggregations cannot form. They are the means for "distance integration" by which the fishes are brought into proximity with one another.

The manner in which the eyes function in bringing about such integration is as yet largely a matter for conjecture. Lyon (1904, 1905) has shown that stream fishes keep their location in the rapidly flowing current by maintaining the retinal image of the objects on the bank in a fixed position. Here the fish move so as to keep the whole background in the line of vision. Brown and Hatch (1929) in an analysis of the reactions of gyrinid beetles, have shown that they give the "fright" reaction to a stimulus which increases the complexity of the visual field, as when a white spot is introduced upon a black background or vice-versa. The aggregations of these beetles also disperse in the dark. A normal young catfish invariably turns and follows another fish swimming in the direction opposite its own, or even in a direction at a slight angle to that of its course. If two fishes are put into a tub at opposite ends, they will remain separate until by chance they come within two or three feet of each other; then one swims directly toward the other and follows it. This same response is given if a rough black paraffin model of a fish or any small object of about the same size is drawn past an individual. In this case the fish ceases to follow the model after a few feet. It seems as if the reaction in

a catfish were a combination of the type described by Lyon and that described by Brown and Hatch. The stimulus is given by the appearance in the field of vision of the configuration of a small moving object. The fish responds by attempting to keep this object in a fixed position on its retina. Uvarov (1928) describes a similar reaction for grasshoppers:—"A sudden movement of an object in the field of vision of a hopper results almost invariably in a reflex jump." These jumps stimulated by moving companions and occurring in the same direction as that of the movement of the stimulating individual, Uvarov believes, cause mass movements of the bands of nymphs. Whether the visual reactions to a small moving object on the part of the young catfish is an inherited reflex or a conditional response has not yet been determined.

To large moving objects, a moving hand for instance, appearing in the field of vision, the fish responds by turning in the opposite direction. This type of behavior is similar to that described by Garrey (1905) for sticklebacks, and explained by the fact that the motion of a near object causes an apparent motion of the background in the opposite direction, and stimulates the fish to keep the retinal image of this background in a constant position. There seems to be a difference in the response of catfish to moving objects of different sizes. Just where the line of division comes has not been investigated.

Since Parker (1910) had shown that the ears, the lateral line organs, and the skin are all receptors of vibrations, but that there are differences in the frequencies of vibrations to which they are sensitive, these three sense organs were studied together in an effort to see whether vibrations play any role in integration in addition to that played by vision. When the fishes were blinded a large percentage of positive reactions was still given when two fish passed within two inches of each other. The stimulus which seems most probably the one working in this case is from the vibrations set up by the tails of the swimming fishes which vibrate approximately six times per second, a frequency to which Parker found the skin responsive. The results with animals on which certain senses had been eliminated by operation indicated that the skin was the organ concerned. The destruction of the lateral line organs had no effect upon the percentage of reactions while the anaesthetizing of the skin reduced the number to such a small percentage that the responses may well have been only apparent, as it is entirely possible that a fish may occasionally turn toward another by chance when no stimulus is received. Responses to vibrations are not important as integrating factors, and are not sufficient to produce aggregations in the absence of vision, as fishes soon separate from each other when blinded. The orientation of fishes through the reception of such stimuli is not possible with any degree of accuracy for a blinded fish rarely makes more than one correct turn toward a fish.

Uvarov cites another interesting case as reported by Vayssière (1921), where movements resulting in animal groupings have been described for the grasshopper, *Dociostaurus maroccanus*. An adult of this species may take off when another individual flies above it, although it will not respond to a stone thrown overhead. A sudden approach to such an insect also results in a jump. This reaction is apparently not due to sight for Lepiney (1928) found that blinded locusts responded to such an approach but that normal individuals put behind a glass did not. In both of these cases vibrations could stimulate a positive response. Whether such stimuli alone can hold together a band of locusts has apparently not been determined.

The skin, in addition to its function of receiving the stimuli of vibrations, is the means by which the strongly positive thigmotropic appetite of these animals is satisfied. That this tropism is an extremely important one in the individual reactions of these fishes has been shown clearly by Schiche (1921), who found that it was surpassed only by negative chemotropism to harmful substances, and equalled in strength the negative phototropism of these fishes. But thigmotropism is not the only response concerned in the aggregations of catfishes. Fishes in older stages which are not actively aggregating nearly always rest in contact with one another, with the tips of the barblets, the ends of the fins or the tail resting against a companion. In two small aquaria, 10 in. by 8 in. by 8 in., each containing three catfishes which were no longer aggregating, observations were made daily for six days, and the position of the fishes was recorded. These aquaria were supplied with sandy bottoms and several plants so that there was plenty of opportunity to satisfy thigmotactic responses without contact with other fishes. Of the twelve observations made, however, ten showed the three fishes in contact or nearly so, while in the other two cases two were in contact and one isolated. The cases where the fishes were not quite in contact may be explained by the fact observed many times that often two fishes come to rest in contact and then drift slightly apart without moving. In six observations made on one pair of fishes, three showed the fishes in contact and three separated. These observations indicate that the aggregating behavior of the active young has its counterpart in the quieter behavior of older fishes, and that here it is quite clearly a contact response with some discrimination, for the fishes rest more frequently in contact with each other than with other objects.

In normal aggregating there is a constant pushing throughout the cluster. Fishes on the outside push in toward the center, pushing out others which immediately push back into the group. This pushing was not as evident in the highly stimulated animals observed in the experimental tub under an overhead light as in a quiet aquarium, but when the skin was anaesthetized before the fishes were placed under observation the pushing was more marked. From an anthropomorphic viewpoint it looked decidedly as if the fishes were trying to get a stimulus which was not produced as easily as usual. This

response to contact does not seem to be due to touch alone. A normal catfish will approach a freshly killed one and push against it persistently, even though there is no possibility of reciprocal behavior on the part of the dead animal. But if a paraffin model of a fish is supplied, although the approach of the active fish is the same, it turns away after dragging the barblets over the model once. The barblets are covered with taste buds, as Herrick (1902) has demonstrated. The tactile-gustatory response is not species specific for a catfish will push against a resting goldfish or mud minnow as readily as against another catfish. The goldfish or mud minnow, however, responds by swimming away and no aggregation is formed.

Contact then is extremely important in these catfish aggregations. The observations so far seem to indicate that it serves both as a means of integration, and still more fundamentally as the principal basis of the social appetite. The satisfaction of this appetite in these distinctly social animals is apparently obtained chiefly through thigmotactic and gustatory stimuli. The reaction given to vibrations by blinded fishes may be only a thigmotactic response also; at least the stimulus for it is received through the skin. The question as to whether such a contact response is the all-important one as well as that of the origin of the visual reaction must be answered by a determination of the part which conditioning plays in this whole behavior pattern. Fishes clearly have the ability to learn as has been shown by Churchill (1916), Hineline (1927), and others. The young of Ameiurus are kept in the nest by one or both of the parents where they are in constant contact with one another for several days, and where there is an opportunity for the development of conditioned automatisms. A slight amount of evidence is at hand indicating that the responses of blinded fishes to vibrations from other fishes is lost during isolation. This is indicated by Series IX and X or the gradient tank experiments where blinded fishes after isolation responded negatively to the end containing the group of fish. But this whole subject needs further investigation before any definite conclusions can be drawn. The writer's results should be interesting in view of the fact that catfish aggregations present an example of a very simple type of vertebrate society. The reciprocal pushing of individuals apparently gives a much greater thigmotactic stimulus and may produce conditioned automatisms which result in the tendency toward group formation.

That physical contact is an important factor in many aggregations has been brought out by Allee (1927) in his survey of the field of animal aggregations. This has been shown by his investigations on land isopods (1926) and the ophiuroid, *Ophioderma brevispina* (1927). In both of these animals aggregations occur under adverse conditions, and, at least in the case of the isopods, are in part due to responses to environmental factors, but as far as reactions to other individuals of the species are concerned the aggregations of both are responses to contact. In the case of the isopods trial and

error movements are made by individuals until contact occurs, after which the animals remain together in an aggregation. Bunching in such animals has survival value because it markedly decreases the rate of water evaporation and lowers the respiratory rate. Ophioderma will aggregate with glass rods in a typical fashion when marine eel grass or other more favorable elements of the substratum are lacking. Although the reciprocal element is not as important among ophiuroids and isopods as in catfishes, for with them aggregations occur in the presence of plants, yet there are evidences that it plays some part, as the effect of glass rods on the respiratory rate of Ophioderma does not equal the effect of the presence of other ophiuroids. A similar case is described by Krizenecky (1923) for the annelid, *Enchytraeis humicultor,* where temporary contact aggregations are produced by vigorous stirring.

The pioneer work in an analytical study of the beginnings of social behavior in animals was that of Szymanski (1913). This investigator distinguishes two types of social behavior reactions: (1) primary reactions which are defined as the sum total of individual reactions apart from any social influence, and (2) secondary reactions which have arisen as a result of long living together of many individuals. To distinguish these he first found all the possible individual reactions to different environmental stimuli. If there was a residue remaining over these primary reactions he designated this a secondary reaction. He found that nest building in the ermine-moth, Hyponomeuta, could be explained entirely on the basis of one primarily reaction, a negative stereotropism. In the formation of eating aggregations of *Hylotome ustulata,* he found primary reactions resulting from three tropisms, positive phototropism, negative geotropism, and positive stereotropism. In addition he found a synchronism in the reactions of the whole colony to the stimulus of shaking, which he believed might indicate a residue over the individual reactions and therefore be a secondary reaction. Since these caterpillars are in contact around the edge of the leaves, the means of integration is probably contact.

From the analysis of the responses concerned in the aggregating behavior of catfishes it is possible to distinguish several secondary reactions which are given by individuals exclusively to other fishes, or possibly to stimuli which have come to be associated with other fishes, and which remain as a residue over the individual reactions. These include the responses to visual stimulation given by small moving objects of about the same size and moving at approximately the rate of a small catfish; the responses of blinded fishes to vibrations set up by other passing fishes; and the responses to pressure and some chemical stimuli. All of these are not species specific. The most exclusively social reaction is the reciprocal pressure given to one catfish by another. Whether different species of Ameiurus will react in a reciprocal fashion to each other is still to be experimentally tested.

The most extensive classification of animal groupings has been made by Deegener (1918) who differentiates his two main divisions on the basis of value accruing to the individuals from the group. Those aggregations with no determinable value he terms accidential associations while groups with some value to the individual are termed societies or essential aggregations. The determination of the presence or absence of value is a difficult one as Deegener recognized. In a later paper (1919) he adds a third division, instinct societies, to include associations where the only value accruing is a satisfaction of the social instinct. This psychic factor Deegener considers of great importance. One aspect of it is what he calls "national feeling" which he believes he has demonstrated for certain arthropods. He found (1919) that mixed families of young of the same species of the arachnid Epeira, remained together in as peaceful a state as a single sympaedium. When families of different species were mixed, however, they separated out in a short time. This illustrates the "national feeling" within a species. In larvae of *Malacosoma castrense* a group which had undergone the first moult separated from one which had not, but the same groups after the moult of the younger individuals mixed freely. In this species Deegener has shown by experimentation that the sense of feeling received through the hairs of the body is very acute, but he still thinks this is not sufficient to explain the behavior observed, and that there is a psychic element present.

The aggregations of young catfishes are clearly societies according to Deegener's system, since there is an evident protective value, as well as a social value shown by the satisfaction of a contact appetite. While the young remain in the nest with the father they form with the male a primary patropaedium. When they leave the nest they form at first a primary sympaedium as long as members from the same family remain together. But since scattering occurs in the dark the aggregations are usually secondary sysympaedia, made up of individuals from several families which have come together secondarily. These groups are homotypic and reciprocal since all members of the aggregation benefit from the grouping. Groups which have been brought into the laboratory from different collecting grounds in the same locality will fuse readily, and the same is true of groups which have been kept apart in the laboratory for some time. This is true even when there is considerable variation in size between the individuals of the two groups provided only that both groups are still actively aggregating. There is therefore no evidence of what Deegener calls the "national feeling" within different groups of this species. No work has been done with other species of catfishes. Schultz (1926) in a study of a similar type of aggregation in young sticklebacks concludes that they are held together by a "necessity for association." It seems possible that with analysis a more concrete cause might be found in this case also.

That physiological state has an important bearing upon aggregations in different groups of animals has been extensively demonstrated. In an analysis of a large aggregation of the stream isopod, *Asellus communis* Say, found in nature Allee (1929), found that differences in activity and reaction habits correlated with differences in metabolic rate and associated with sex caused a great preponderance of males in these aggregations. He had previously shown (1912) by laboratory experiments that breeding conditions markedly affect the rheotaxis of this species. On the other hand bunching itself has been found to be a factor in determining the metabolic rate of animals. Thus isolated, starving Ophioderma (Allee, 1927) when compared with groups show a higher initial respiratory rate, a more rapid decrease, and a much lower final rate.

In the case of catfishes Eddy (1925) has shown that increasing or decreasing the metabolic rate by means of stimulants or depressants accordingly intensifies the closeness of aggregations or scatters them. Determinations of oxygen consumption (Eddy, 1926) showed that individuals from an aggregation have a higher rate of respiration than isolated individuals. Fishes isolated from an active group have a higher rate than individuals found in natural isolation.

The metabolic rate of young animals is generally higher than that of older individuals which would naturally give rise to greater activity, other conditions being equal. This finds a parallel in the fact that aggregations of young more active catfishes satisfy a contact appetite in motion while the more sluggish adults satisfy this appetite by often resting together. Fishes not aggregating in the aquarium will invariably aggregate when stimulated by a strong light. Such behavior seems to be the result of increased metabolic rate. These facts indicate that active aggregations and high metabolic rate are closely correlated. What the effect of resting aggregations has upon the respiration of the individuals concerned has not been determined.

A somewhat similar relation between stimulation and aggregation apparently exists among grasshoppers from the facts cited by Uvarov. Grassé (1923) has shown that reflex reactions of Acrididae, even of the non-gregarious species, are more energetic if several individuals are subjected to the same experiment together. Temperature is a very important factor in such cases as the movement of bands often occurs with rises in temperature, Sviridenko (1924) describes how swarms disperse after the final moult, and how at the same time non-social stimuli produce less response in the adult than in immature grasshoppers. Uvarov believes that reactions of solitary grasshoppers to stimuli do not differ greatly from those known in the gregarious locusts, except that there is no accumulation of nervous tension which leads to mass movements in them.

From the present investigation it is possible to draw certain conclusions concerning the behavior of young catfishes during the daily cycle. In the

evening as soon as it begins to grow dark the catfish minnows separate and swim about sweeping through the water or along the bottom with their barblets. With the highly developed taste buds over the entire body and the acute sense of touch, eyesight is, as Herrick (1902) has concluded, unimportant for feeding. Blinded fish exhibit activity similar to this in the light. The supposition that night is the normal feeding time is supported by the fact reported by fishermen that catfish and bullheads begin to bite at dusk. As soon as it starts to grow light in the early morning the young fishes come together into aggregations and remain thus during the entire day, reforming in a short time if they are scattered by a disturbance. Some feeding may occur while the fishes are aggregated but it is doubtful if this is true to any extent. Usually they are in a close group, actively pushing against each other or resting at the surface in contact or close proximity.

The comparison of the type of grouping found among catfishes with the schooling common among many species of pelagic fishes is an interesting one. Parr (1927) on the basis of much observation and some experimentation upon several species of schooling fishes has found a satisfactory explanation of this phenomenon in the assumption of a simple automatic "attraction" toward a perceived companion. This "attraction" consists of two simple antagonistic responses, a bending of the course toward the individual and an adjustment of its position to one parallel to that of the companion. These two reactions permit an explanation of the normal forward moving schools and also the milling phenomena. He concludes: "By the recognition of such tropisms or set of automatic responses to the separate perceptions of single individuals only, all peculiarities of the normal school may be satisfactorily explained without necessitating the assumption of deliberate purposeful activities or general 'social instincts,' giving complicated responses to stimulations from the entire school as a unit." By experimentation he has shown that these reactions are not given by blinded fishes, and so concludes that visual responses are the only ones concerned. He advances the supposition that the schools disperse at night, as has been concluded in the case of catfishes from this investigation. He cites the case of the catfishes and the bullheads as a probable exception to the importance of eyesight in aggregations. Because of the compactness of the schools, the highly developed sense of touch, and the poor eyesight, he believes that the tactile sense may here be the important one for aggregations with eyesight probably playing a secondary role. He has underestimated the importance of eyesight in catfishes, but is correct in his estimation of the importance of tactile responses.

Parr considers the reactions to visual stimuli which are involved in the schooling of fishes as inherited instincts, which in the light usually surpass the feeding and breeding instincts. It is quite possible similarly to conclude in the case of the catfishes that responses to contact with those to visual stimuli, either inherited or acquired by conditioning, overcome during the day

the feeding reactions in the young fishes. All of the pelagic fishes which Parr has observed have exceptionally large eyes and he believes these may be responsible for the importance of vision in their behavior. This suggests to one's mind the situation among the insects where exceptionally large eyes result in a definitely directed tropistic response to light in many species. In these cases responses to usual stimuli seem to dominate the individual. In catfishes, we have a group of fishes with unusually small eyes for this class. These eyes are functional as shown clearly by reactions to visual stimuli, but it is doubtful if these responses are as important as in other groups of fishes. The catfishes are, however, unique in their lack of scales and in the abundance of touch and taste organs situated all over their bodies and with specially developed barblets for the perception of tactile and gustatory stimuli. Their aggregations are of a type based upon contact responses, and it seems possible that these may dominate other behavior. Their reactions are complicated, as vision also plays an important role; but, in addition pressure, taste, and vibratory stimuli are also concerned.

The possible method of evolution of such social reactions as occur among catfishes is not difficult to conceive. Parr notes that all of the schooling pelagic fishes are defenseless. The catfishes have an efficient defense mechanism in the sharp spines of the fins with which they can inflict a considerable wound. But aside from this they are unusually defenseless and a desirable prey. Their bodies are soft and scaleless and the usual swimming of the young is performed slowly and steadily. An obvious protective value of the aggregating behavior is evident if one attempts to catch one fish from a group. The rapid scattering makes it impossible to keep one individual in view. The slippery bodies increase the difficulty. A single fish, however, is an easy prey. During the night this group protection is not needed as far as animals hunting by sight are concerned. Their dark color renders catfishes inconspicuous, and their highly developed tactile organs must give instant warning of any foreign body. In the laboratory blinded fishes at any sudden contact give a rapid avoiding reaction which is probably typical for normal fishes in the dark. In the light the many eyes of the group compensate for the rather poorly developed eyes of the individual. The sudden movement of one fish induces movement among all the members of the group, resulting in dispersal and escape. Thus these groups have made a beginning of a division of labor. Such protective attributes of bunching may well serve as the mechanism of natural selection by which the aggregating behavior has appeared. In the case of the pelagic fishes it is a sight reflex complex which has evolved. In the catfishes, where a group of responses concerning several sense organs is at work with conditioning possibly playing a large part in the individuals' reactions, a strong positive contact appetite may have been the factor selected. So far as known the catfish type of aggregation that has been described and analyzed is peculiar to the silurids, and appears to be associated

with the highly developed sense organs which are important here. The question of phylogenetic versus ontogenetic development of the social instinct in these fishes awaits experimental evidence.

In addition to the survival value of aggregations due to protection as suggested, there are other possibilities, evidence for which is less apparent on the surface but which have been demonstrated already for a large number of species. These are the beneficial effects of crowding which are being shown to exist for an increasing number of species and in an extended variety of conditions. A large amount of this work has been carried on by Allee and his students in this country and by Drzewina and Bohn in Europe. Experiments to test out this aspect of catfish aggregations have not been made as yet, but it seems quite possible that some protection of this kind may be present here.

Finally, in these societies of young catfish as in other sympædia the impulses leading to aggregations are entirely divorced from sex drive or sexual significance. These groups consist of sexually immature young catfishes whose social appetites are diffuse but based primarily upon reciprocal positive contact responses. Such a basis for social life is not very different from the tropholaxis which Wheeler (1923) believes is the foundation for the societies among the social insects. The importance of this contact factor is also consistent with the number of aggregations, especially among the simpler animals, which are integrated entirely by contact with distance perceptors playing no part.

SUMMARY

The young of *Ameiurus melas* (Rafinesque) give evidence of a positive response to highly conditioned water to which they have become adapted when this is run against unconditioned water in a gradient tank. They do not respond, however, to any moderate amount of conditioning, even when this is much greater than any amount which could be acting in producing in aggregations. The cutting of the olfactory nerves has no effect upon the positive reactions to other fishes in either blinded or normal individuals. A chemical factor which could be perceived through the olfactory organs is therefore probably not concerned in aggregating behavior.

Vision is an important factor in the integration of these aggregations. Neither blinded fishes nor normal fishes in the dark ever aggregate, and normal fishes follow a small moving object in a way which, if continued, would result in aggregation formation.

An individual when blinded responds positively in a large percentage of cases to another fish in motion at a distance of less than two inches, probably by detecting the vibrations set up by the tail of the other fish. This reaction is not affected by the destruction of the lateral line organs, but is almost eliminated when the skin is anaesthetized with magnesium sulphate.

To actual contact catfish give a positive response involving some ability to discriminate but not between fishes of their own and another species. Responses to contacts which probably involve both gustatory and thigmotactic stimuli received through the skin may be the primary factor underlying the social appetite which results in aggregations in this species.

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